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Antoni STACHURSKI, Jerzy R. ZIMKA

Department of Plant Ecology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny (near Warsaw), 05-092 Łomianki, Poland

THE BUDGET OF NITROGEN DISSOLVED IN RAINFALL DURING ITS PASSING THROUGH THE CROWN CANOPY IN FOREST ECOSYSTEMS*

ABSTRACT: By using new techniques for rain-water collecting, and the multiple regression method it has been demonstrated that hydrological factors and the amount of water falling through and that being intercepted by the canopy have no significant effect on the budget of the nitrogen dissolved in the throughfall. The budget is controlled by two biotic factors, the actions of which are opposite: the activity of phytophages which enriches rain water with dissolved nitrogen, and the canopy absorption, due to which there occurs a high decrease in nitrogen content in this water (on an average by 80%).

KEY WORDS: Forest ecosystems, nitrogen, precipitation throughfall, budget, absorption, phytophagous fauna, leaching, washing, aerosols.

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1. INTRODUCTION

The first stage of nitrogen cycling in forest ecosystems is the passing of the nitrogen dissolved in rain water from the atmosphere through the canopy layer. If this process is considered in terms of budget, then the empirical data found in the literature indicate that all the three possibilities may occur here. Nitrogen budget may be positive – more nitrogen leaves the canopy layer than is brought into it from the atmosphere (Nihlgärd 1970, Eaton, Likens and Bormann 1973, Sollins et al. 1980). It may be negative, sometimes very highly so (Ulehlova, Klimo and Jakrlova 1976, Herrera and Jordan 1981), as well as assume values approaching zero (Carlisle, Brown and White 1966, Denaeyer-De Smet 1969, Nihlgärd 1970). All the three budget situations may also be realized in the same ecosystem analysed in a temporal aspect (Herrera and Jordan 1981).

A positive budget is usually interpreted as resulting from the leaching of nitrogen from the forest vegetation, or washing off of the aerosols intercepted by the canopy (Nihlgärd 1970, Eaton, Likens and Bormann 1973, Likens et al. 1977, Melillo 1981). According to a number of authors, a negative budget indicates absorption of nitrogen from the rain by the canopy (Carlisle, Brown and White 1966, Miller et al. 1979, Herrera and Jordan 1981).

It seems that these concepts do not cover all the possible causes that might account for the nitrogen budget under consideration. In the case where more nitrogen leaves the canopy with rain water than is brought in from the atmosphere, a hypothesis equally probable as the leaching of nitrogen from the vegetation, or washing off of aerosols, is the assumption that this is caused by the action of phytophages: damage to foliage, leaching from the faeces of phytophages, and from the faeces of their predators and the like. Studies of the budget of dissolved nitrogen in the throughfall omit the effect of this biotic factor, and even if a study programme includes the role of phytophages in the overall nitrogen cycling processes, the activity of the phytophages is not simultaneously related to the nature of the budget discussed (Gosz, Likens and Bormann 1972, Eaton, Likens and Bormann 1973).

The aim of the present study was to determine the factors governing the budget of the nitrogen dissolved in rain water in the phase of its passing through the forest canopy layer, with a special attention focussed on the role of phytophages in these processes.

2. STUDY AREA, MATERIAL AND METHODS

The studies were carried out in two parts of Poland: in the woods of the Kampinos Forest in 1979 and 1981, and in the Masurian forests in 1980. The study area included 9 forest plant communities representing five units: Vaccinio myrtilli-Pinetum, Pino-Quercetum, Tilio-Carpinetum, Circaeo-Alnetum and Carici elongatae-Alnetum. The

communities under study grew in loose sands, and in medium sand or clay soils. Investigations were carried out from April until November. In each of the forest ecosystems studied 10 rain gauges were then fixed under the canopy. Simultaneously, to determine the amount of nitrogen brought in with the rain from the atmosphere, analogous rain traps were put up in a woodless area, usually in a clearing bordering the forest communities under study.

The new type of rain gauge used in the study has been described in detail in a separate paper (S t a c h u r s k i and Z i m k a 1982). It consists of a polyethylene collector of the capacity of 2 l of water, and a polyethylene funnel, 10 cm in diameter, with two different filters (Fig. 1). The upper filter was a plastics grid 1 mm in mesh diameter. The lower filter fixed at the end of the funnel was a type GF/F or GF/B Whatman glass filter with a retention capacity of 0.7 or 1.0 μm. The function of the upper filter was a preliminary filtration of the rain – holding back larger particles, whereas the glass filter with a high retentivity screened off all particles of 1 μm–1 mm in section, letting only dissolved substances into the water collector. To prevent the evaporation of ammonia nitrogen (NH_3–N) and the growth of microflora, which also can cause nitrogen losses, to each rain collector an amount of chemically pure salicylic acid was added. This ensured a constant maintenance of the pH of the solution at about 2.7, which practically eliminated the growth of microflora and ammonia nitrogen evaporation.

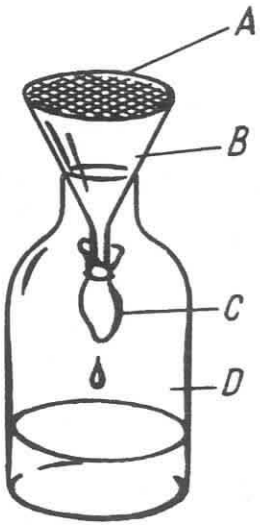

Fig. 1. The rain trap used in field studies
A – plastics grid ~ 1 mm in mesh diameter, B – plastics funnel, C – GF/F Whatman filter of 0.7 μm retention, D – plastics container

Since the studies were also to evaluate the amount of carbon dissolved in the rain water, a parallel methodical option was used: this consisted in the application of rain gauges of an analogous type to which no salicylic acid was added.

The rain gauges were emptied at one-month intervals. The water contained in each gauge was measured and the glass filter was replaced with a new one of a known weight. Because part of the fine particles passing through the polyethylene funnels were

deposited on their walls, all the funnels were weighed, and it was thus possible to apply a correction to the amount deposited on the filters.

In the laboratory, the water was filtered through a nylon net which held back any excess of salicylic acid in the form of undissolved crystals (incomplete dissolution of salicylic acid occurred very rarely, only in the case of a very poor precipitation). The glass filters were dried at 65 C for 48 hours and then weighed to the nearest 0.01 mg.

The use of methods of this type made possible a precise determination of the amount of dissolved nitrogen brought by the rain to the forest ecosystems. Owing to the use of high-retentivity filters in the gauges, dissolved nitrogen fraction was at once separated from the undissolved fraction (the nitrogen contained in the dusts) under field conditions, and not, as in the case of other methods, in the laboratory, after a many-days' field exposure. This is important on account of the fact that during the field exposure dissolved nitrogen may pass into an organically bound form (bodies of microorganisms), particularly if the growth of microorganisms in the gauges is not controlled. Because of this, filtering of the water in the laboratory may lead to a considerable underestimation of the amount of dissolved nitrogen, and the level of underestimation may be variable, depending on the rate of multiplication of the microorganisms under field conditions.

Another significant factor resulting from the methods employed was the possibility to assess the activity of the phytophages. The upper filter in the rain gauges had been so selected experimentally that it let through only the fine amorphous material such as the faeces of the phytophages, holding back larger morphous parts such as spruce needles, small scales, seeds or fragments of bark and lichen litter. The dynamics of the fall of parts < 1 mm determined for the Kampinos Forest by these methods shows a very clear peak in the spring months (Fig. 2) which coincides with the abundance dynamics of the leaf-eating entomofauna at the same study sites (K a c z m a r e k and W a s i l e w s k i 1977). A phytophagous origin of the particles collected is also confirmed by the chemical analysis. Nitrogen concentration in this material is very high – $2.80 \pm 0.40\%$, similar to the content of nitrogen in the leaves eaten by the phytophages – $2.72 \pm 0.46\%$. This made it possible to relate the chemistry of the throughfall to the number of particles sedimented on the glass filter, and consequently to determine the effect of phytophages on the amount of elements transferred to the cycle with rain water.

The preliminary chemical preparation was so adjusted that the gas chromatographic method could be used for the determination of carbon and nitrogen content in water samples. As the Carlo Erba's elementary analyser analyses only solid samples, dissolved carbon and nitrogen had to be transformed into the solid state. This was done by a slow evaporation of the water samples at a temperature of about 50°C. The low evaporation temperature and the high acidity of the water samples (pH 2.7) prevented the evaporation of ammonia nitrogen. As shown by calculations on the basis of the dissociation constants of water and ammonia, at the given levels of pH and evaporation temperature $1.82 \cdot 10^{-4}$ per cent of ammonium nitrogen could be in the non-dissociated phase. Thus as little as 0.0002% of the total ammonium nitrogen could pass into the

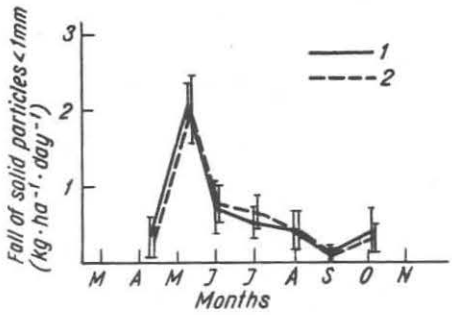

Fig. 2. Falling dynamics of amorphous parts < 1 mm intercepted by rain traps in the associations of Kampinos Forest in 1981 ($\bar{x} \pm SD$)
1 – Tilio-Carpinetum association, 2 – Pino-Quercetum association

gaseous phase (NH_3) and represent a potential cause of losses of this element, which is an extremaly small error, not affecting the results.

Evaporating was carried out in three replications in 100 ml evaporating dishes of known weights: about 80 ml of water was poured into each dish and then the dish was weighed with an accuracy to the nearest 0.01 mg. After evaporating to the dry state the evaporating dish was weighed again with the same accuracy. In this way information was obtained on the total concentration of all substances (organic and inorganic therein carbon and nitrogen) in 1 l of water. The standard error of the estimation of this parameter was small, ranging from 1 to 2%.

At the next preparatory stage the appropriate dry weight amount of the material for analyses – the remainder after evaporation – was obtained. For this purpose several litres of water was evaporated in 0.5 l evaporating dishes and then the dry sediment was removed from the walls (if teflon evaporating dishes are used, the process is very easy). The amount removed was not checked for quantity, the only objective being to collect a sufficient amount of material for analyses. The material so obtained was homogenized, dried again and analysed on a Carlo Erba's elementary analyser, using a weighed portion of 1 mg, the standard weighed portion for this apparatus, weighed with an accuracy to the nearest 0.001 mg. As the concentration in $mg \cdot l^{-1}$ of the dry residue after water sample evaporation was already known, and so was the percentage of nitrogen in it, it was possible to obtain the concentration of nitrogen in water samples by multiplying these two quantities.

The above-presented methodology using gas chromatography for the elementary composition is characterized by a very high sensitivity not obtainable by other methods. Practically nitrogen can be detected over the range of concentration of < 0.0001 to $> 10\,000$ $mg \cdot l^{-1}$. The accuracy of the analyses is high, the standard error ranging from 1 to 2%, and is comparable to that obtained by other methods for the determination of nitrogen in waters, e.g., the colorimetric methods (G o l t e r m a n 1971). This level of accuracy is determined by the standard error of the estimation of the

concentration of the dry residue after water sample evaporation. The standard error of the estimation of the content of nitrogen in samples ensured by the elementary analyser is considerably lower: < 0.3%. The methods for nitrogen content measurement used in the present study show its total amount in water samples. It is the sum total of organic, ammonium, nitrite and nitrate nitrogen. This results from the very high temperature of sample burning in the elementary analyser – about 1200°C. At this temperature even the hardest to decompose forms of nitrate nitrogen pass into the gaseous form.

3. INPUT OF NITROGEN DISSOLVED IN RAIN WATER FROM THE ATMOSPHERE AND ITS BUDGET IN THE COURSE OF ITS FALLING THROUGH THE CANOPY IN VARIOUS FOREST ECOSYSTEMS

As has already been mentioned, studies of the budget of dissolved nitrogen during the passing of precipitation through a forest canopy were carried out in different parts of Poland: in the Masurian forests and in the woods of the Kampinos Forest. The forest ecosystems under study belonged to different phytosociological units. This approach made it possible on the one hand to find the possible differences in the input of dissolved nitrogen brought in from the atmosphere by precipitation, and on the other – to follow the possible differences in the budget of the nitrogen input from the atmosphere, related to the type of an ecosystem.

The amounts of dissolved nitrogen input to the forest ecosystems from the atmosphere during the growing season have been set out in Table I. The amounts are found to vary. To the woods of the Kampinos Forest as little as several kilogrammes of nitrogen in water solutions is input from the atmosphere during the growing season: 3.8–5.3 $kg \cdot ha^{-1} \cdot$ growing $season^{-1}$. The input to the Masurian forests amounts to 21.8 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$. The rate of nitrogen input from the atmosphere to the zones analysed also varies. The input of nitrogen from the atmosphere to the woods of the Kampinos Forest remains at a more or less stable level, without any distinct peak during the growing season, whereas the input to the Masurian forests is on an average higher and attains a clear peak in July – as high as about 10 kg $N \cdot ha^{-1} \cdot month^{-1}$ (Fig. 3). Thus the zones under study differ considerably in respect of both the amount of nitrogen brought in with the precipitation and the seasonal rhythm of this input to forest ecosystems.

Considerable differences are also seen in the nature of the budget of dissolved nitrogen in the phase of its passing through the canopy. In the woods of the Kampinos Forest the budget is positive: more nitrogen leaves the canopy with the throughfall than is brought in from the atmosphere. For the Masurian forests a clearly negative budget is found: considerably less nitrogen leaves the canopy than has been brought in with rainfall from the atmosphere (Table I). The nature of the budget itself seems not to be related to the species inhabiting an ecosystem. For instance, in the Kampinos Forest a forest association is distinguished with the pine clearly dominant where a positive

Table I. Amount of total nitrogen dissolved in rainfall and input to forest ecosystems in different parts of Poland, and the amount of nitrogen in the throughfall in different types of forest associations (the amount of nitrogen is given in kg·ha^{-1}·growing season^{-1}: April – November) ($x \pm SD$)

A – Carici elongatae-Alnetum, CA – Circaeo-Alnetum, PQ – Pino-Quercetum, TC – Tilio-Carpinetum, TC^1 – pine and spruce in oak-hornbeam habitat, VmP – Vaccinio myrtilli-Pinetum

Elements compared	Kampinos 1979			Kampinos 1981			Masuria 1980		
Input of N dissolved in rainfall (A)	3.84 ± 0.36			5.26 ± 0.29			21.84 ± 1.25		
N dissolved in throughfall (T)	9.76 ± 0.65	9.17 ± 0.91	8.42 ± 1.10	6.03 ± 0.31	5.52 ± 0.46	7.87 ± 0.83	11.68 ± 0.60	13.50 ± 0.77	13.67 ± 1.10
Budget N (T – A)	5.92 ± 0.75	5.33 ± 0.98	4.58 ± 1.16	0.77 ± 0.43	0.26 ± 0.54	2.61 ± 0.88	– 10.16 ± 1.39	– 8.34 ± 1.46	– 8.17 ± 1.67
Dominant species in stand	pure pine stand	hornbeam, alder, pine, linden	pure alder stand	pine, oak, hornbeam	hornbeam, pine, birch	alder, hornbeam	pine, spruce	linden, pine, aspen	hornbeam, pine, oak, spruce
Phytosociological type	VmP	TC	A	PQ	TC	CA	TC^1	TC	TC

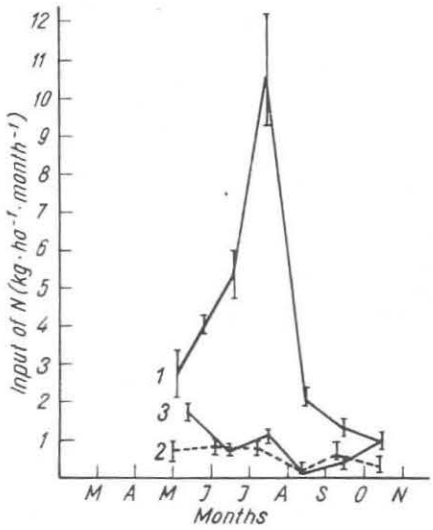

Fig. 3. Rate of input of total nitrogen dissolved in rainfall to forest ecosystems during the growing season (April-November) ($\bar{x} \pm 50$)
1 – Masuria 1980, 2 – Kampinos 1979, 3 – Kampinos 1981

Table II. Comparison of total nitrogen input with rainfall and the amount of nitrogen contained in the throughfall in Kampinos forests
For the comparison of the significance of the means compared Student *t*-test for correlated data was used

Sampling period	Dissolved N in rainfall ($kg \cdot ha^{-1}$)	Dissolved N in throughfall in particular forest associations ($kg \cdot ha^{-1}$)		
		pure pine stand VmP	hornbeam, alder, pine, linden TC	pure alder stand A
18 Apr. – 14 May 1979	0.63	1.95	1.55	1.89
14 May – 18 June	0.98	1.93	2.27	1.43
18 June – 26 July	1.06	3.25	3.00	2.79
26 July – 24 Aug.	0.20	1.03	0.95	0.62
24 Aug. – 26 Sept.	0.69	1.23	1.09	1.12
26 Sept. – 29 Oct. 1979	0.28	0.37	0.31	0.57
$\bar{x}$	0.64	1.52		
SD	0.33	0.89		
r	0.85			
n	18			
t	5.761			
p	<0.01			

nitrogen budget is found. In the Masurian region a pine-spruce ecosystem similar to that mentioned above in respect of dominance has a clearly negative nitrogen budget – about 10 kg N·ha^{-1}·growing season^{-1} less nitrogen leaves the canopy than is brought in from the atmosphere (Table I). The only primarily suggestible regularity is a probale correlation between the amount of nitrogen coming from the atmosphere and the nature of the budget discussed. For it can be seen that where the input of nitrogen from the atmosphere is low, the budget is positive, and if the input of nitrogen from the atmosphere is high, the budget values are clearly negative, irrespective of the forest ecosystem type (Table I).

A spatial and temporal analysis also confirms this regularity. In the woods of the Kampinos Forest, where the input of nitrogen from the atmosphere is low, the amount of dissolved nitrogen in the throughfall is consistently higher throughout the growing season, and in all the forest associations analysed than the input from the atmosphere. In the Masurian forests the amount of nitrogen in the throughfall is in almost all cases lower than its input from the atmosphere. Student t-test analysis for correlated data has shown that two cases are statistically significant at the level of 0.01 (Tables II, III).

Table III. Comparison of the amount of total nitrogen input with rainfall and the amount of nitrogen in the throughfall in Masurian forests

For the comparison of the significance of the means Student *t*-test for correlated data was used

Sampling period	N from atmosphere (kg·ha^{-1})	N in throughfall in particular forest associations (kg·ha^{-1})		
		pine, spruce TC[1]	linden, pine aspen TC	hornbeam, pine, oak, spruce TC
25 Apr. – 15 May 1980	1.82	0.91	0.69	0.78
15 May – 4 June	2.52	2.90	3.36	2.83
4 June – 4 July	5.36	1.47	2.41	2.80
4 July – 24 July	7.09	2.08	2.34	3.02
24 July – 6 Sept.	2.95	2.65	2.35	2.36
6 Sept. – 2 Oct.	1.09	0.95	1.53	1.09
2 Oct. – 6 Nov. 1980	1.01	0.72	0.82	0.79
$\bar{x}$	3.12	1.85		
SD	2.17	0.92		
r	0.57			
n	21			
t	3.125			
p	<0.01			

The above analysis has shown that the amount of nitrogen brought with precipitation into forest ecosystems may differ considerably: by several-several dozen kilogrammes. The budget of dissolved nitrogen passing through the canopy may vary in its nature: it may be negative or positive. The nature of the budget does not seem to be related to any specific type of plant association, but more likely to the value of the input from the atmosphere.

4. FACTORS CONTROLLING THE BUDGET OF DISSOLVED NITROGEN IN THE PHASE OF ITS PASSING THROUGH THE CANOPY

One of the simplest factors affecting the budget of nitrogen during its passing through tree crowns could be hydrological factors, i.e., the amount of water falling through or retained by the canopy. It may be expected that the amount of water in the throughfall will act towards an increase in the content of nitrogen in it. The budget would then tend to be more and more positive if the amount of water in the throughfall increased. Such a supposition would agree with the views found in the literature according to which nitrogen can be leached from forest vegetation. The process of water interception by the canopy could account for situations where the budget in question takes negative values. For this reason an analysis was carried out for the degree of correlation between the nitrogen budget studied and hydrological factors.

The results obtained have not confirmed any leading role of these factors in the control of the budget under investigation. The degree of correlation between nitrogen budget and the amount of water intercepted by the tree crowns is low: $r = -0.31$, being statistically insignificant (Fig. 4). A rather low too correlation coefficient has been obtained for the relationship: nitrogen budget-the amount of water in the throughfall $r = -0.59$. The following direction has been found for this relationship: the larger the throughfall, the more nitrogen is absorbed by the canopy (Fig. 5). Although the correlation coefficient obtained is statistically significant at the level of 0.01, the direction of the relationship is quite unexpected, and has no logical justification in the possible mechanism of action of a factor such as the falling of water through tree crowns. It indicates a fortuitous rather than a biological nature of the relationship found.

Thus the preliminary analysis has not revealed any clear role of hydrological factors in the control of the budget of dissolved nitrogen during its passing through the canopy. Certainly, it does not rule out the effect of these factors entirely, for in accordance with the rules of correlation any factor analysed individually may not show a statistically significant effect, but when analysed in conjunction with other factors, it may show such an effect. Nevertheless, the analysis shows that hydrological factors are not the main factors ordering the empirical data obtained concerning the nitrogen budget considered.

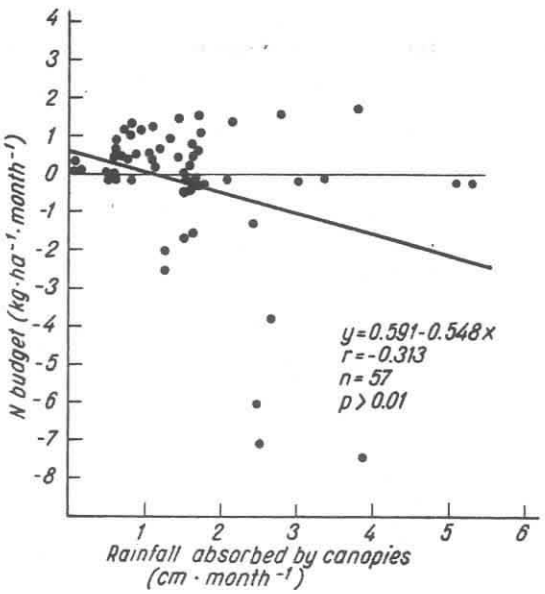

Fig. 4. Relationship between the amount of rainfall absorbed by the canopy (x) and the budget of nitrogen dissolved in the throughfall (y) (for all forest associations studied per growing season: April – November)

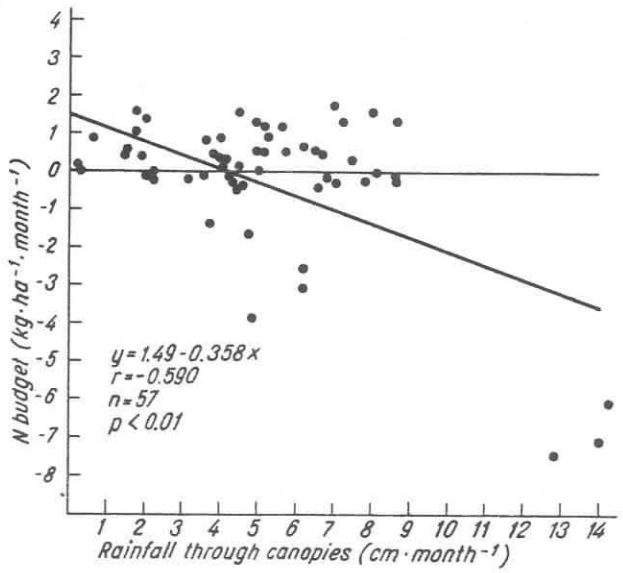

Fig. 5. Relationship between the amount of throughfall (x) and the budget of nitrogen dissolved in the throughfall (y) (for all forest associations studied per growing season: April – November)

In the preceding section a supposition has been put forward that the nature of nitrogen budget may be correlated with the amount of dissolved nitrogen supplied to forest ecosystems from the atmosphere. For this reason, a spatio-temporal analysis was carried out for the nature of the relationship between the amount of nitrogen input from the atmosphere and the budget of this nitrogen after its passing through the canopy. The degree of correlation between these two variables has been found to be high: $r = -0.88$ and statistically significant at the level of < 0.001. The following relationship is realized: if the input of nitrogen from the atmosphere is low, nitrogen budget is positive, whereas with an increasing nitrogen input from the atmosphere it becomes more and more negative (Fig. 6). The positive nitrogen budget values for a range of low values of nitrogen input from the atmosphere are not fortuitous. The a coefficient in the regression equation has a positive value and differs significantly from zero at the level of 0.01.

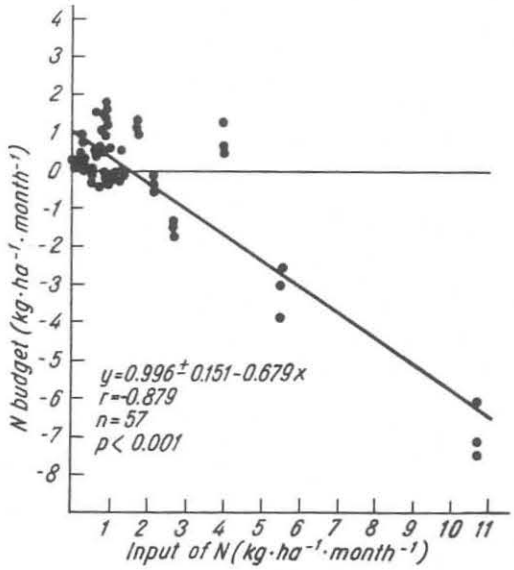

Fig. 6. Relationship between the amount of total nitrogen dissolved in rainfall input from the atmosphere (x) and the budget of nitrogen dissolved in the throughfall (y) (for all forest associations studied per growing season: April – November)

A similar relationship is realized in the tropical rain forest, that is, under the conditions of quite a different climatic zone and a different specific composition of the plants. Similarly, correlated by the present authors H e r r e r a' s and J o r d a n' s (1981) data indicate that the greater the input of nitrogen from the atmosphere, the more negative its budget during its passing through the canopy. The correlation coefficient is high: $r = -0.93$ and statistically significant at the level of 0.001 (Fig. 7). In this case also the a coefficient of the regression equation is positive and significantly different from zero at the 0.01 level of confidence, which indicates that this relationship does not pass across the zero xy axis.

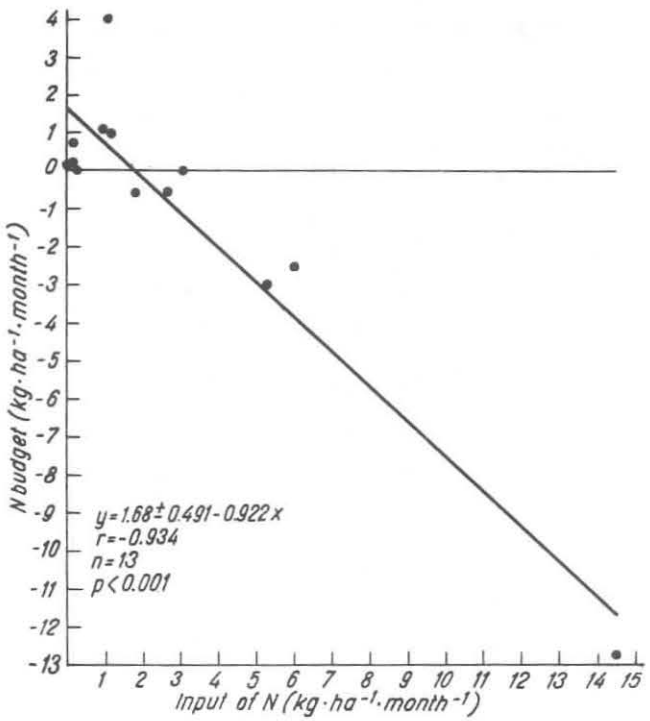

Fig. 7. Relationship between the amount of nitrogen input from the atmosphere (x) and the budget of nitrogen in the throughfall (y) (relationship realized in a tropical rain forest in Rio Grande – calculated on the basis of Tables II, III – Herrera and Jordan 1981)

The relationships presented for temperate zone woods and tropical rain forests are similar enough to be included in one common regression. Although the material merged is so diverse, the coefficient obtained is high: $r = -0.90$ and statistically significant at the level of < 0.001 (Fig. 8). This shows that the course of the processes taking place in the canopy of temperate zone woods and tropical rain forests when nitrogen dissolved in rain water passes through it is similar.

For a yet better authentication of this relationship, literature data available to the authors and their own results have been set out in the following way: nitrogen input from the atmosphere-budget of nitrogen in the throughfall. This was only done in a spatial aspect. For the summary included budget results or budget values, for the growing season in different types of forest associations, and their comparison with the quantity of nitrogen input from the atmosphere. Although the material analysed included forest associations very different phytosociologically, the correlation coefficient obtained was high: $r = -0.86$ and statistically significant at the level of < 0.001. The relationship found is of the same direction as in the previous cases: for low quantities of nitrogen input from the atmosphere the nitrogen budget is positive, and as the quantity of nitrogen input from the atmosphere increases, it becomes more

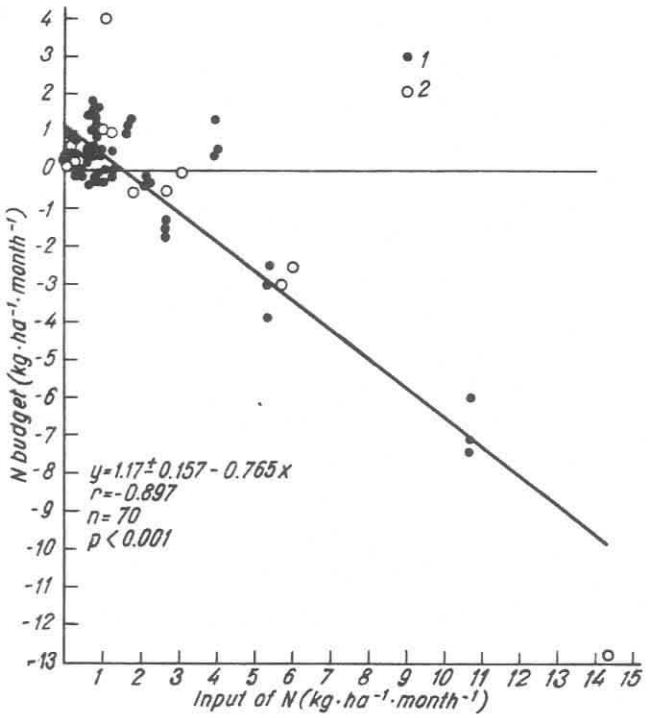

Fig. 8. Relationship between the amount of nitrogen input from the atmosphere (x) and the budget of nitrogen in the throughfall in forest ecosystems (y)
1 – temperate zone forests (the authors' own data), 2 – tropical rain forest in Rio Grande (H e r r e r a and J o r d a n 1981)

and more negative. In this combination too the a coefficient in the regression equation is positive and significantly different from zero at the level of 0.01 (Fig. 9).

It seems therefore that irrespective of the phytosociological type and climatic zone, in forest ecosystems a similar regularity is realized in time and space: the budget of dissolved nitrogen in the throughfall is negatively correlated with the quantity of nitrogen input from the atmosphere. Thus the quantity of nitrogen input from the atmosphere is a factor that orders the data on the nitrogen budget studied more strongly than do the hydrological factors analysed before; the correlation coefficients obtained are much higher.

A question suggests itself as to what is the biological implication of the relationship found, the nature of which is so general. If the a coefficients in the regression equation were equal to zero, and the regression line passed across the zero xy axis, then the biological interpretation would be very straight-forward. As the rainfall passes through the crown canopy the nitrogen dissolved in it is absorbed. This absorption occurs at a constant rate relative to the quantity of nitrogen input from the atmosphere, e.g., at the rate of $-0.7x$, which means that 70% of nitrogen is absorbed during the passing of rainfall through the canopy. As a result, a growth in nitrogen input from the

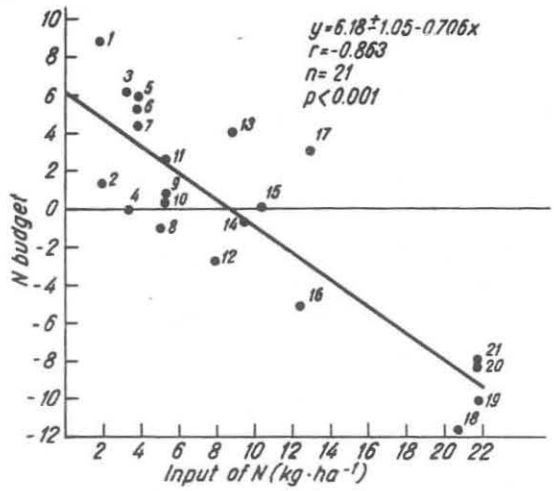

Fig. 9. Relationship between the amount of nitrogen input from the atmosphere (x) and nitrogen budget in the throughfall (y)

Relationship established on the basis of data reported by the following authors: 1 – Eaton, Likens and Bormann (1973), 2 – Sollins et al. (1980), 3–4 – Nihlgärd (1970), 5–7 – results from the present study, 8 – Miller et al. (1979), 9–11 results from the present study, 12 – Foster and Morrison (1976), 13 – Mitchel, Waide and Todd (1975), 14 – Carlisle, Brown and White (1966), 15 – Denaeyer-De Smet (1969), 16 – Ulehlova, Klimo and Jakrlova (1976), 17 – Henderson and Harris (1975), Henderson et al. (1978), 18 – Herrera and Jordan (1981), 19–21 – results from the present study

atmosphere is followed by an increase in the absolute value of nitrogen absorption by the canopy, and consequently the nitrogen budget becomes more and more negative.

However, as has been shown by the above analysis, the a coefficients of the regression equation are greater than zero, due to which for a low nitrogen input from the atmosphere the budget assumes at first positive values, and then only for an increased input does it take more and more negative values. This picture cannot be explained solely by nitrogen absorption in the canopy, but further assumptions must be made.

Theoretically, the budget of each element may be the resultant of many coinciding or opposite processes. So it is possible to make a preliminary assumption that in addition to the absorption of nitrogen from the rainfall, which no doubt takes place in the canopy, there is another permanently acting factor of an opposite nature – enriching rain water with nitrogen as it passes through the canopy. It is such a factor that would cause a shift of the regression line from point zero xy towards positive values. This factor might be, in addition to those suggested in the literature: the leaching of nitrogen from foliage and washing-off of the nitrogen aerosols absorbed by the canopy, the activity of phytophages.

In the forest ecosystems under investigation the activity of phytophages, as measured by the amount of their faeces collected by the rain traps described earlier,

remained at a fairly constant level: 165.7 + 26.28 kg·ha^{-1}·growing season^{-1}. It was therefore a factor of a similar intensity of action and a low variation from ecosystem to ecosystem – about 16%. In this connection the multiple regression method was used to determine the effect of phytophage activity on the nitrogen budget discussed. Nitrogen input from the atmosphere, for which a strong action has been revealed in the analysis made so far, was included as another variable. Since their effect could not be entirely ruled out, hydrological factors were also included in the analysis as variables. Thus the effect of a total of 4 independent variables was studied: amount of water intercepted by the canopy (x_1), amount of throughfall (x_2), phytophage activity (x_3) and nitrogen input from the atmosphere (x_4). The following polynomial was used as the describing equation: $y = a + b_1x_1 + \ldots + b_4x_4$. The results of this analysis have been presented in Table IV. A very high coefficient of multiple correlation has been obtained: $R = 0.96$ statistically significant at the level of < 0.001. It has been found that hydrological factors: amount of water intercepted (x_1) and falling through the canopy (x_2) have no significant effect on the nitrogen budget. Their action appears to be weak and statistically insignificant – $p > 0.05$. The effect of phytophage activity (x_3) and that of nitrogen input from the atmosphere (x_4) are statistically significant at the level of < 0.001.

Table IV. Coefficients of multiple regression equation for the budget of nitrogen in the throughfall (y) in relationship to hydrological factors (x_1, x_2), phytophage activity (x_3) and nitrogen input from the atmosphere (x_4) (on the average for all the forest association types studied per growing season)
$N = 57$, y – budget of dissolved nitrogen in the throughfall (kg·ha^{-1}·month^{-1}), x_1 – amount of rainfall absorbed by the canopy (cm·month^{-1}), x_2 – amount of throughfall (cm·month^{-1}), x_3 – fall of phytophage faeces (kg·ha^{-1}·month^{-1}), x_4 – input of dissolved nitrogen from the atmosphere (kg·ha^{-1}·month^{-1})

	R	a	b_1x_1	b_2x_2	b_3x_3	b_4x_4
	0.957	−0.0230	0.0580	0.0219	0.0395	−0.811
SE	0.012		0.0840	0.0302	0.0042	0.0445
t	79.750		0.691	0.727	9.401	18.219
p	<0.001		>0.05	>0.05	<0.001	<0.001

As the effect of hydrological factors was insignificant, a new, reduced regression equation was derived, leaving out these variables (Table V). An identical coefficient of multiple regression was obtained: $R = 0.96$, which indicates that the joint effect of both hydrological factors also was statistically insignificant. So the final multiple regression equation describing the budget of dissolved nitrogen in the throughfall takes the following form:

$$y = 0.157 + 0.0358x_1 - 0.786x_2 \quad (1)$$

where y is the nitrogen budget in kg·ha^{-1}·month^{-1}, x_1 – phytophage activity measured by the amount of faeces produced in kg·ha^{-1}·month^{-1}, x_2 – nitrogen input from the atmosphere in kg·ha^{-1}·month^{-1}. Both factors are statistically

Table V. Coefficients of multiple regression equation for the budget of nitrogen in the throughfall (y) dependent on phytophage activity (x_1) and nitrogen input from the atmosphere (x_2) (an average for all the forest association types studied per growing season)

$N = 57$, y – budget of dissolved nitrogen in the throughfall (kg·ha^{-1}·month^{-1}), x_1 – fall of phytophage faeces (kg·ha^{-1}·month^{-1}), x_2 – input of dissolved nitrogen from the atmosphere (kg·ha^{-1}·month^{-1})

	R	a	b_1x_1	b_2x_2
	0.958	0.157	0.0385	−0.786
SE	0.011		0.00393	0.0319
t	87.091		9.796	24.639
p	<0.001		<0.001	<0.001

significant at the level of < 0.001. Their action is opposite: in the regression equation they have the plus and minus signs, which confirms earlier suppositions concerning the causes of the differences in the nitrogen budged studied. Thus phytophage activity enriches the throughfall with dissolved nitrogen, while the absorption process in the canopy reduces the content of nitrogen in it. The latter process is very intensive, and the coefficient $-0.79x$ obtained indicates that almost 80% of the nitrogen input from the atmosphere is intercepted by the canopy.

The equation derived contains a constant: value of the a coefficient $= 0.157$ which is added to the effect of factors x_1 and x_2. Most likely this represents a constant, unknown input of nitrogen in the amount of 0.157 kg·ha^{-1}·month^{-1}, maybe in form of aerosol nitrogen, enriching the throughfall, but not included in the independent variables analysed.

The above regression equation was derived "jointly" for all forest ecosystems which consisted of entirely different phytosociological units. It is therefore interesting to see how great is the variation of the coefficients obtained for phytophage activity and crown canopy absorption. The measure of this variation is the standard error showing how different they are: spatially (between ecosystems) and temporally. This analysis indicates that both the canopy absorption coefficient and the phytophage activity coefficient are little variable. The variation found for canopy absorption is -0.79 ± 0.03, that is, of the order of 4%. The standard error for the effect of phytophages is 0.0385 ± 0.00393, that is, 10%. This indicates that they are factors of a stable, little variable intensity, and that their effect is similar in all the ecosystems studied, although their phytosociological structure is different. It is probably because of this, that so high a correlation coefficient: $R = 0.96$, has been obtained in spite of the fact that the regression equation was derived jointly for all, sometimes quite different phytosociological units.

A correlation coefficient of this order, where $R^2 = 0.92$ informs that the regression equation derived includes 92% of the causes of differences of the budget analysed. The remaining 8% unaccounted for includes ecosystem and temporal variation of the factors considered, other factors not covered by the equation, and of course the error of assessment of the particular parameters (laboratory and field). It is very unlikely that

this error, especially the field error, is much below 8%, which would indicate that the equation presented includes the majority of, if not all, the causes of the phenomenon considered.

In view of this, the possible effect, so readily raised by many authors, of the washing away of aerosols from the leaves on the budget of nitrogen (N i h l g ä r d 1970, E a t o n, L i k e n s and B o r m a n n 1973, L i k e n s et al. 1977, M e l i l l o 1981) seems to be quite doubtful. One might perhaps expect the effect of this factor only in the range of 2–3%, as there must be some, not accounted for by the equation, variation connected with the error of assessment of the parameters analysed.

Proof that aerosols, at least in the material used by the present authors, have no effect on the budget studied can be found in quite a different way. Assuming that it is the washing-off of aerosols that enriches the throughfall with nitrogen, we would expect the nitrogen thus transferred to be in inorganic form. And it the source of enrichment of the throughfall is the action of a biotic factor – the phytophages, we may expect this nitrogen pool to be of an organic origin. In this connection an analysis was made for the relationship between the concentration of nitrogen dissolved in the throughfall and the concentration of organic carbon dissolved in it. A high correlation has been found between these two elements: the higher the concentration of dissolved carbon, the higher the concentration of nitrogen in the throughfall (Fig. 10). The correlation coefficient is very high: $r = 0.98$ and statistically significant at the level of < 0.001. The relationship is linear, and the regression line exactly crosses the zero xy axis, since the value of the a coefficient in the equation is not significantly different: $t_a = 0.18$, $p > 0.05$.

The source of the nitrogen dissolved in the throughfall is mainly some dissolved organic matter, which rules out a major contribution of aerosols to the enrichment of this water with nitrogen. And the fact, shown by the multi-factor analysis, is confirmed that this enrichment is caused by a biotic factor.

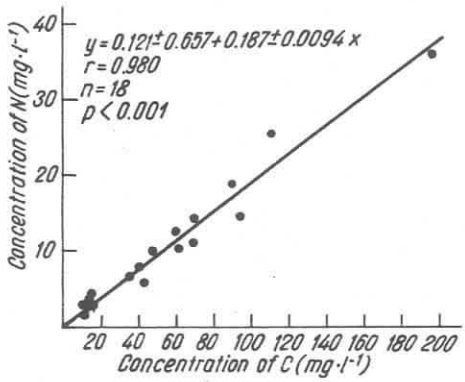

Fig. 10. Relationship between the concentration of carbon dissolved in the throughfall (x) and the concentration of dissolved nitrogen (y)
Relationship established on the basis of experiments carried out in Kampinos forests in 1979

The role of the nitrogen aerosols intercepted appears thus to be small, and it seems to provide only the background for the processes going on in the canopy. This background is most likely captured by the *a* coefficient of the regression equation. The main factors controlling the budget of the nitrogen passing through the canopy are biotic processes: canopy absorption and the action of phytophages.

5. THE MECHANISM OF POSITIVE AND NEGATIVE BUDGETS OF NITROGEN DISSOLVED IN THE THROUGHFALL

In the preceding section it has been shown that the passage of nitrogen through the canopy layer can be successfully described with an equation in which the budget of dissolved nitrogen is the function of phytophage activity and canopy absorption of nitrogen. By using this equation and empirical data on the activity of phytophages, and nitrogen input from the atmosphere it is possible to calculate a theoretical budget for an ecosystem and compare it with the budget found empirically. So it is possible to reconstruct, as it were, the mechanism bringing about a specific type of budget in forest ecosystems. Of particular importance are extremely different budgets, that is, a strongly positive and a strongly negative budgets. As has been shown in the present study, budgets of this type occur in forest ecosystems in a situation where the input of nitrogen from the atmosphere varies considerably. It has been calculated how a specific budget of dissolved nitrogen in the throughfall is brought about when nitrogen input from the atmosphere is low (3.8 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$) and when it is high (21.8 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$).

As a comparative unit two oak-hornbeam forest associations of a similar species structure of the stand were taken. For the calculations the following modified version of equation (1) was used:

$$y = 0.0052 + 0.0385\,x_1 - 0.786\,x_2 \qquad (2)$$

where y is the budget of nitrogen in the throughfall in $kg \cdot ha^{-1} \cdot day^{-1}$, x_1 and x_2 – the effects of phytophages and conopy absorption, respectively, on nitrogen budget. The value of a – 0.0052 represents some permanent nitrogen input to forest ecosystems, most likely of aerosol type – in $kg \cdot ha^{-1} \cdot day^{-1}$. This form of the equation in terms of budget calculation per day is more convenient than equation (1), because the time of sample collecting in the field was not always exactly 30 days.

The results of the calculations have been presented in Tables VI, and VII and in Figure 11. If nitrogen input from the atmosphere is low, the theoretical budget is as follows. Canopy absorption removed 3.01 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$ from the throughfall. Phytophage activity enriched it with nitrogen by 7.86 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$. An unknown, probably aerosol input of nitrogen caused an additional increase in its content by about one kilogramme during growing season. This resulted in a positive budget of +5.85 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$. The empirical value was similar: 5.33 kg $N \cdot ha^{-1} \cdot$ growing $season^{-1}$ (Table VI, Fig. 11). As a result, 9.69 kg of

Table VI. Calculation of theoretical budget of dissolved nitrogen in the throughfall in an oak-hornbeam association under conditions of low nitrogen input from the atmosphere = 3.84 kg N·ha^{-1}·growing season^{-1} and phytophage activity = 204.2 kg faeces·ha^{-1}·growing season^{-1}
Calculations based on empirical phytophage activity and empirical nitrogen input from the atmosphere and made by using equation (2)

Study period	Days	Empirical input (kg·ha^{-1}·day^{-1})		Factors affecting N budget			N budget (kg·ha^{-1})	
		phyto-phage faeces x_1	N from atmos-phere x_2	phytophages $0.0385\,x_1$	canopy absorption $-0.786\,x_2$	aerosol N? 0.0052	y'	y''
18 Apr. – 14 May 1979	26	0.50	0.024	0.50	−0.49	0.14	0.15	0.92
14 May – 18 June	34	2.21	0.029	2.89	−0.77	0.18	2.30	1.29
18 June – 26 July	38	1.37	0.028	2.00	−0.84	0.20	1.36	1.94
26 July – 24 Aug.	28	0.77	0.007	0.83	−0.15	0.15	0.83	0.75
24 Aug. – 26 Sept.	32	0.86	0.022	1.06	−0.55	0.17	0.68	0.40
26 Sept. – 26 Oct. 1979	30	0.50	0.009	0.58	−0.21	0.16	0.53	0.03
			Total	7.86	−3.01	1.00	5.85	5.33

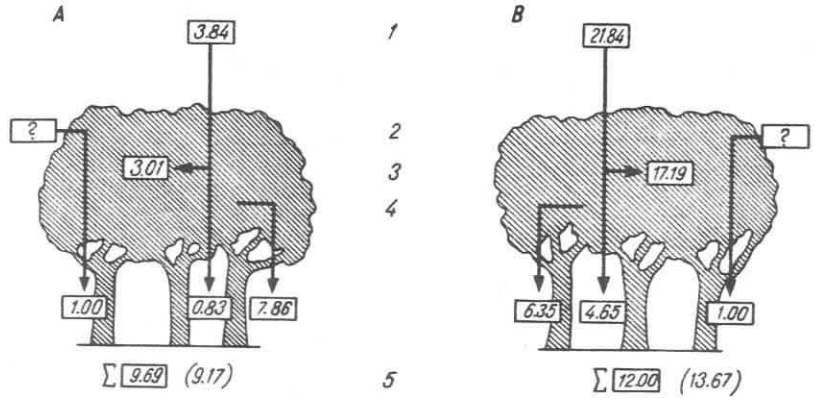

Fig. 11. Diagram showing the occurrence of positive and negative budgets of nitrogen dissolved in the throughfall in oak-hornbeam associations (kg dissolved N·ha^{-1}·growing season^{-1})
A – under low nitrogen input conditions, B – under high nitrogen input conditions, (–) empirical value of throughfall, 1 – input of N via rainfall, 2 – unknown N input, possibly of aerosol origin?, 3 – absorption of N contained in rainfall, 4 – N in water due to phytophage activity, 5 – total N in throughfall

dissolved nitrogen, according to theoretical computation, or 9.17 kg, as found empirically, was input to the ecosystem cycle, and not 3.84 kg nitrogen, that is, the quantity input from the atmosphere (Fig. 11).

If the input of nitrogen from the atmosphere is high, the budget is quite different. Canopy absorption attains a high level of absolute values: 17.19 kg·ha^{-1}·growing season^{-1} of the nitrogen input from the atmosphere is intercepted. Phytophages enrich the rainfall by 6.35 kg of dissolved nitrogen, and the aerosol input by ~1 kg N·ha^{-1}·growing season^{-1}. All in all, the theoretical budget is strongly negative: −9.84 kg N·ha^{-1}·growing season^{-1}. Negative also is the empirical budget: −8.17 kg N·ha^{-1}·growing season^{-1} (Table VII). As a result, only 12 kg, and not 21.84 kg of dissolved nitrogen reaches the forest floor, the amount determined empirically being 13.67 kg of nitrogen (Fig. 11).

The above comparison shows the mechanism leading to a positive or negative budget in forest ecosystems. With a similar intensity of phytophage activity, a low input of nitrogen form the atmosphere brings about a situation where the canopy absorption of nitrogen, as expressed in absolute values, attains a low level that is of little little significance for the total budget. In such a situation the enrichment of rainfall with nitrogen due to phytophage activity "predominates" quantitatively, and a positive nitrogen budget is observed. In this case plant systems lose more nitrogen because of phytophages than they gain by way of absorption processes. If there is a high nitrogen input from the atmosphere, then absorption processes begin to predominate quantitatively, the budget becomes negative, and in the overall gain-loss squaring the plant communities "gain" nitrogen in spite of the activity of phytophages.

The above-presented mechanism bringing about a positive or negative budget of the nitrogen passing through the canopy is characteristic of a more or less stable and

Table VII. Calculation of theoretical budget of dissolved nitrogen in the throughfall in an oak-hornbeam association under conditions of high input of nitrogen from the atmosphere = 21.84 kg·ha^{-1}·growing season^{-1} and phytophage activity = 164.9 kg faeces·ha^{-1}·growing season^{-1}

Study period	Days	Empirical input (kg·ha^{-1}·day^{-1})		Factors affecting N budget			N budget (kg·ha^{-1})	
		phyto-phage faeces x_1	N from atmos-phere x_2	phytophages 0.0385 x_1	canopy absorption −0.786 x_2	aerosol N? 0.0052	y'	y''
25 Apr. – 15 May 1980	20	0.52	0.091	0.40	−1.43	0.10	−0.93	−1.04
15 May – 4 June	19	2.10	0.133	1.54	−1.99	0.10	−0.35	0.31
4 June – 4 July	30	1.24	0.179	1.43	−4.22	0.16	−2.63	−2.56
4 July – 24 July	20	1.01	0.355	0.78	−5.58	0.10	−4.70	−4.07
24 July – 6 Sept.	42	0.85	0.070	1.37	−2.31	0.22	−0.72	−0.59
6 Sept. – 2 Oct.	26	0.59	0.042	0.59	−0.86	0.14	−0.13	0.00
2 Oct. – 6 Nov. 1980	34	0.18	0.030	0.24	−0.80	0.18	−0.38	−0.22
			Total	6.35	−17.19	1.00	−9.84	−8.17

low foliage consumption by phytophages, that is, a situation generally observed in forest ecosystems. This situation may, however, be easily altered as soon as the activity of phytophages attains a sufficiently high level. Even at a very high level of nitrogen input from the atmosphere there may arise conditions under which budget under study will be positive. For example, calculations made by using equation (1) show that with a level of nitrogen input from the atmosphere of 22 kg·ha^{-1}·growing season^{-1}, and faeces production of about 500 kg·growing season^{-1} ($\sim$30% of foliage consumption), nitrogen budget will attain positive values. In this case a very strong canopy absorption will be dominated by a yet stronger phytophage activity. The whole passage of dissolved nitrogen through the crown canopy takes place in a dynamic system where plants actively intercept the pool of nitrogen entering the forest ecosystems, whereas the activity of phytophages goes in the opposite direction: they force part of the nitrogen pool from plants and return it to the cycle among other things in dissolved form. All this depends on the quantitative ratio of these two biotic components.

6. DISCUSSION

The lack, demonstrated in the study, of a significant effect of hydrological factors on the budget of dissolved nitrogen in the throughfall represents further orientation of literature views concerning the possibility of nitrogen leaching from plants. Simultaneously, the group of views are confirmed, according to which nitrogen is an element strongly chemically-bound with organic matter, not being subject to the effect of hydrological factors, and therefore not leached from green leaves (G o s z et al. 1975), or from leaves that are turning yellow (Z i m k a and S t a c h u r s k i 1980), nor from dead leaves (M o r t o n 1977).

According to the results of the present study, 92% of the budget of atmospheric nitrogen in the throughfall is dependent on two factors: a strong, on the average eighty-per cent canopy absorption of nitrogen and a factor whose action is opposite – the activity of phytophages which enriches rainfall with dissolved nitrogen of organic origin. In the non-industrial zones under study canopy-intercepted aerosols of nitrogen represent only a small background of these processes.

The effect of phytophages enriching the rainfall with organic nitrogen seems to be of many-sided nature. Firstly, the appearance of nitrogen dissolved in water may be the result of leaching of readily dissolving nitrogen compounds from phytophage faeces, e.g., nitrogenous metabolites which phytophages expel together with faeces (N a k a n o and M o n s i 1968). Secondly, this nitrogen may be also a metabolite of predators as a result of phytophage consumption in the grazing food chain in the canopy. Thirdly, it may even be a plant nitrogen washed out of damaged leaves.

From the point of view of the role of phytophages in the transfer of nitrogen to the forest floor, it is not immaterial whether all the forms of transfer are effected simultaneously, or whether some of them are not realized at all. If it appeared, for

instance, that there is also an indirect effect of phytophages via plants, e.g., due to nitrogen leaching from leaves damaged by them, then the classical assessment, only on the basis of consumption measurement, of the role of phytophages in nitrogen cycling would lead to its underestimation. Conversely, if we assume, for instance, that all dissolved nitrogen input to the cycle is derived from leaf-leaching, which is not true, then relating the consumption of nitrogen by phytophages to nitrogen content in the throughfall is an overestimation of the role of phytophages in the supply of nitrogen to the forest floor. Further investigations into this problem will no doubt have to be made to make it possible to ultimately decide whether the role of phytophages in the transfer of nitrogen can be determined by the classical estimation of consumption.

Another factor, in addition to the activity of phytophages, affecting the input of nitrogen dissolved in water to the forest floor is the absorption of nitrogen by the canopy. Both field studies and experimental data confirm the occurrence of a phenomenon of this type in forest ecosystems (Carlisle, Brown and White 1966, 1967, Lang, Reiners and Heier 1976, Ulehlova, Klimo and Jakrlova 1976, Herrera and Jordan 1981, Jakucs et al. 1981). In laboratory experiments both ammonium- and nitrate nitrogen were found to be quickly taken up by the leaves (Lang, Reiners and Heier 1976). Nitrogen absorption by the plant tissues was found not only in tree foliage, but also in various epiphytic species living in tree crowns. From the possibility that nitrogen can be taken up by both the canopy components: leaves and epiphytes, the question arises as to which of them is responsible for the overall absorption of nitrogen from the rainfall. In the literature no information can be found on this subject, conclusions can only be drawn on the basis of the quantitative ratios of the two components. Epiphyte biomass may amount to 850 $kg \cdot ha^{-1}$ (Lang, Reiners and Pike 1980). The average foliage biomass is about 3880 $kg \cdot ha^{-1}$ (Zimka and Stachurski 1976). However, on the assumption that the area ratios will be of the same proportions, the positive dominant of the canopy is the leaves, and it seems that it is on this component that the absorption of nitrogen from the rainfall primarily depends.

Nitrogen absorption from the rainfall seems to be wide-spread in forest ecosystems. The fact that in the field studies carried out so far such phenomena, especially those of several-dozen per cent intensity, were recorded rather rarely should be ascribed to the specific mechanism bringing about the nitrogen budget under consideration. Namely, over low values of nitrogen input from the atmosphere nitrogen absorption is masked by the opposite process of rainfall enrichment with nitrogen due to the activity of phytophages. This makes impossible their direct detection by methods of the budget type, and moreover, it suggests the acceptance of the aerosol or leaf-leaching origin of the nitrogen enriching the rainfall. Only by applying the multiple regression methods, or working out the budget of dissolved nitrogen in the throughfall against a wide gradient of nitrogen input from the atmosphere (as has been set out in Fig. 9 on the basis of data reported by different authors) can one arrive at the conclusion that nitrogen is absorbed at a high rate from the rainfall as it falls through the canopy.

The results from the present study have not confirmed the concept of aerosol enrichment of the rainfall with nitrogen. Besides, it is doubtful whether the nitrogen aerosols intercepted by the canopy can to a significant extent enrich the rainfall with nitrogen. For if on an average 80% of the rainfall nitrogen is absorbed by the canopy, it is equally probable that aerosol nitrogen will be absorbed also at a high rate in forest ecosystems. This would be supported by the fact that inorganic compounds of nitrogen are easily dissolved in water. Apart from this, the dew that arises in periods without rain, or the fog that settles on the surfaces of the leaves form a water layer which favours the dissolution of nitrogen aerosols. Conditions therefore arise similar to those occurring during a rainfall.

In this connection it seems that as regards the fate of aerosol nitrogen in forest ecosystems quite a different concept can be adopted than that found in the literature. Nitrogen aerosols are not washed off plant tissues but absorbed by them, and are as a result only to a very low extent input to the ecosystem cycle. If we assume that the coefficient of aerosol absorption by the canopy is equal to nitrogen absorption from the rainfall, that is, 0.8 x where x is the quantity input, then according to the concept adopted we would find that only 0.2 x reaches the forest floor. According to the assumption that aerosols are washed off the foliage by rainfall, the whole amount previously intercepted by the tree foliage surface (aerosols deposited on foliage surface) would reach the forest floor. In this case, too, further investigation is needed to verify the two views.

7. SUMMARY

The effect was investigated of hydrologic and biotic factors on the budget of nitrogen in the throughfall. A new type of rain trap with a double filter system was used (Fig. 1). The traps were set up in open spaces and beneath the canopy. During the growing season 9 forest ecosystems representing five phytosociological units were analysed in the Kampinos National Park and in Masurian forests.

The input of nitrogen in water solutions from the atmosphere was found to range from 3.8 kg·ha^{-1}·growing season^{-1} (Kampinos) to as much as 21.8 kg·ha^{-1}·growing season^{-1} (Masurian region) – Table I. Variable also was the rate of nitrogen input in the zones analysed (Fig. 3). The budget of dissolved nitrogen (the throughfall-the atmosphere) in the forest ecosystems was positive (Kampinos) or strongly negative (Masuria), but no consistent differences could be found related to a particular species structure of the stands (Table I).

Using the multiple regression method, the effect was analysed of four factors on the nitrogen budget discussed: amount of rainfall intercepted by the canopy, amount of water in the throughfall, phytophage activity measured by their faeces biomass, and the quantity of nitrogen input with water solutions from the atmosphere. A very high coefficient of multiple correlation has been obtained: $R = 0.96$, statistically significant at the level of < 0.001. The effect of the amount of intercepted rainfall, and that of the water in the throughfall were found to be statistically insignificant ($p > 0.05$). But significant was the effect of: phytophage activity and quantity of dissolved nitrogen input from the atmosphere ($p < 0.001$ – Table IV). As the activity of hydrological factors was insignificant, a new, simplified regression equation was developed. An identical correlation coefficient: $r = 0.96$ was obtained, and the statistical significance of phytophage activity and quantity of nitrogen input from the atmosphere also was at the level of < 0.001 (Table V). An analysis of the derived equation has shown that the effects of the two factors are of an opposite nature. Phytophage activity

causes an enrichment of the throughfall with nitrogen, while dissolved nitrogen input from the atmosphere is absorbed by the canopy layer in the proportion of $-0.786x$. This means that nearly 80% of the nitrogen input from the atmosphere is absorbed by the canopy, and by as much is the content of nitrogen lowered in the throughfall reaching the forest floor.

The spatial and temporal variation of the factors is narrow. The standard error of the coefficient of the canopy absorption of nitrogen amounts to 4%, and of phytophage activity to 10% (Table V). They are, therefore, factors of a relatively stable action, the intensity of which in ecosystems differing in the species structure of the stand is similar.

The paper explains the mechanisms bringing about a positive or negative budgets of dissolved nitrogen in the throughfall. If the nitrogen input from the atmosphere is low, with a small absolute canopy absorption value, there is a quantitative predominance of rainfall enrichment with nitrogen due to the activity of phytophages. A positive budget is then observed. When the nitrogen input from the atmosphere is high, absorption dominates quantitatively over the enrichment of rainfall by phytophages, and the budget becomes negative (Tables VI, VII, Fig. 11).

The results from the present study show that the passing of nitrogen in water solutions through the canopy is not static in nature, nor is it controlled by hydrologic factors. It is a fully dynamic process controlled by biotic factors, and its final result is determined by the quantitative predominance of either factor, the effect of which is opposite to that of the other: (1) nitrogen absorption by the canopy, and (2) phytophage activity.

8. POLISH SUMMARY

Badano wpływ czynników hydrologicznych i biotycznych na bilans azotu rozpuszczonego w wodach deszczowych przechodzących przez warstwę koron drzew. W badaniach zastosowano nowy typ pułapki deszczowej wyposażony w podwójny system filtracyjny (rys. 1). Pułapki były rozstawione na otwartej przestrzeni i pod koronami drzew. Przeanalizowano w ten sposób w ciągu sezonu wegetacyjnego 9 ekosystemów leśnych należących do 5 jednostek fitosocjologicznych. Badania przeprowadzono na terenie Kampinoskiego Parku Narodowego i lasów mazurskich.

Stwierdzono, że dopływ azotu w roztworach wodnych z atmosfery kształtował się na poziomie 3,8 $kg \cdot ha^{-1} \cdot$ sezon wegetacyjny^{-1} (Kampinos) względnie aż 21,8 $kg \cdot ha^{-1} \cdot$ sezon wegetacyjny^{-1} (Mazury) – tab. I. Różne było również tempo dopływu azotu w analizowanych strefach (rys. 3). Bilans azotu rozpuszczonego (wyjście spod koron drzew – atmosfera) w ekosystemach leśnych był albo dodatni (Kampinos) lub też silnie ujemny (Mazury). Nie zaznaczały się przy tym jakieś konsekwentne różnice w zależności od struktury gatunkowej drzewostanów (tab. I).

Przeanalizowano metodą regresji wielokrotnej wpływ 4 czynników na omawiany biłans azotu: ilości wody intercepowanej przez korony drzew, ilości wody przepływającej przez korony drzew, działalności fitofagów mierzonej biomasą produkowanego kału i wielkości dopływu azotu w roztworach wodnych z atmosfery. Otrzymano bardzo wysoki współczynnik korelacji wielokrotnej $R = 0{,}96$, istotny statystycznie na poziomie < 0.001. Okazało się, że wpływ ilości wody intercepowanej i przepływającej przez korony drzew jest nieistotny statystycznie ($p > 0.05$). Natomiast istotny wpływ mają: czynność fitofagów i wielkość dopływu azotu rozpuszczonego z atmosfery ($p < 0.001$ – tab. IV). Ponieważ działanie czynników hydrologicznych było nieistotne, wyprowadzono nowe uproszczone równanie regresji. Otrzymano identyczny współczynnik korelacji $r = 0{,}96$, a istotność statystyczna działania fitofagów i wielkości dopływu azotu z atmosfery kształtowała się również na poziomie < 0.001 (tab. V). Analiza wyprowadzonego równania wykazała, że charakter wpływu obu czynników jest przeciwstawny. Czynność fitofagów powoduje wzbogacenie wód deszczowych przechodzących przez korony drzew w azot. Natomiast azot rozpuszczony dopływający z atmosfery jest w warstwie koron drzew pochłaniany w relacji $-0.786x$. Oznacza to, że prawie 80% dopływu azotu z atmosfery jest absorbowane w koronach drzew i o tyle są zubożane wody deszczowe dochodzące do dna lasu.

Przestrzenna i czasowa zmienność obu czynników jest niewielka. Błąd standardowy współczynnika absorpcji koronowej azotu kształtuje się na poziomie 4%, działalności fitofagów – 10% (tab. V). Są to więc czynniki o względnie stałym działaniu, mające podobne nasilenie w ekosystemach o różnej strukturze gatunkowej drzewostanu.

Wykazano na czym polega mechanizm powstawania sytuacji dodatniego i ujemnego bilansu azotu rozpuszczonego przechodzącego przez korony drzew. W warunkach niskiego dopływu azotu z atmosfery, gdy zjawiska absorpcji koronowej przybierają w skali bezwzględnej niewielkie wartości, przeważa ilościowo proces wzbogacania wód deszczowych w azot spowodowany czynnością fitofagów. Obserwuje się wtedy bilans dodatni. Natomiast w sytuacji, gdy dopływ azotu z atmosfery jest wysoki, procesy absorpcji dominują ilościowo nad procesami wzbogacania wód deszczowych przez fitofagi i bilans staje się ujemny (tab. VI, VII, rys. 11).

Uzyskane wyniki pokazały, że proces przechodzenia azotu w roztworach wodnych przez korony drzew nie ma charakteru statycznego, nie jest również sterowany czynnikami hydrologicznymi. Jest to proces w pełni dynamiczny, sterowany czynnikami biotycznymi i o ostatecznym jego wyniku decyduje ilościowa przewaga któregoś z przeciwstawnie działających czynników: absorpcji koronowej azotu i czynności fitofagów.

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